ALUMINIUM TOXICITY AND TOLERANCE IN THREE HEATHLAND SPECIES

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Abstract. *Arnica montana* and *Cirsium dissectum* are characteristic species of species-rich heathlands and adjacent grasslands, which declined during the last decades in the Netherlands. It has been shown in a recent field survey that the decline of *A. montana* and *C. dissectum* might be caused by soil acidification. *Calluna vulgaris* is not susceptible to soil acidification. It was hypothesized that increased aluminium concentrations in the soil as a result of acidifying atmospheric inputs caused the decline of *A. montana* and *C. dissectum* whereas *C. vulgaris* would not be sensitive to enhanced aluminium concentrations. We studied the effects of different Al:Ca-ratios and of Al concentrations on the development of *A. montana*, *C. dissectum* and *C. vulgaris* in nutrient solution experiments. All three species showed aluminium accumulation in the shoots related with increased aluminium concentrations in the nutrient solutions. This accumulation was correlated with a reduction in growth when plants were cultured at high Al concentrations (200–500 μmol l^{-1}), in both *A. montana* and *C. dissectum*. In addition, indications of Al toxicity were observed in these plant species, e.g. poor root development, yellowish leaves and reduced contents of Mg and P in the plants. *C. vulgaris* did not show reduced growth or poor plant development due to high Al concentrations. The negative effects of aluminium in *A. montana* and *C. dissectum* were partly counterbalanced when plants were grown on the same Al concentrations but with increased Ca concentrations, resulting in lower Al:Ca-ratios. No effects of enhanced calcium concentrations on *C. vulgaris* have been observed.

Key words: aluminium toxicity, *Arnica montana*, *Calluna vulgaris*, *Cirsium dissectum*, heathland, soil acidification

1. Introduction

In Western Europe, soil acidification and eutrophication occur as a result of atmospheric deposition of SO_x, NO_y, and NH_x. Both are a major threat to biodiversity in many (semi-) natural ecosystems (Bobbink *et al*., 1992). Dwarf-shrub and grassland communities occur at acidic or at slightly buffered soils in the Western-European heathland landscape, and are sensitive to both acidification and eutrophication.

As a result of enhanced nitrogen (N) inputs, the dwarf-shrub dominated communities on acidic soils have been transformed into swards dominated by grasses (Heil and Diemont, 1983; Roelofs, 1986; Aerts and Berendse, 1988). Apart from this transition, a drastic decline in species, such as *Arnica montana* L. and *Cirsium dissectum* (L.) Hill, has been observed in Dutch heathland and adjacent grassland communities at slightly buffered soils. It has been suggested that this decline was caused by acidification as a result of SO_x deposition (Van Dam *et al*., 1986;

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Houdijk *et al*., 1993; De Graaf *et al*., 1994). Field studies have demonstrated that these threatened plants are characteristic of soils in the cation exchange buffer range, with moderate pHs (4.5–6.0), whereas the dwarf shrubs (*Calluna vulgaris* (L.) Hull and *Erica tetralix* L.) mainly grow on acidic soils in the aluminium buffer range (Hayati and Proctor, 1990; Houdijk *et al*., 1993). In a field survey it was shown that *A. montana*, one of the endangered species, recently disappeared from sites which have nowadays soil pH values below 4.5 and with raised aluminium (Al) concentrations (Fennema, 1992).

Al toxicity after soil acidification is a widely observed phenomenon and it is generally assumed that Al^{3+} is the phytotoxic form (Foy *et al*., 1978; Ryan *et al*., 1994). The detrimental effects of high Al^{3+} concentrations have been shown particularly in forest ecosystems (e.g. Ulrich, 1983; Boxman *et al*., 1991; Andersson and Brunet, 1993). The effects of Al^{3+} can be diminished by high concentrations of divalent base cations, such as calcium (Ca) and magnesium (Mg) (Korcak, 1990; Ryan *et al*., 1994).

We hypothesize that increased soil Al concentrations after acidification are the major cause of the decline of the threatened plant species from these slightly buffered communities. In the present study, an analysis is given of the growth response to increasing Al concentrations and to different Al:Ca ratios in a nutrient-solution experiment. The shoot and root biomass of two seriously threatened forbs (*A. montana* from dry and *C. dissectum* from wet conditions) have been studied, in contrast to those of the characteristic dwarf shrub *C. vulgaris*. At the end of the experiment, nutrient contents of the plant material were determined and the results are discussed.

2. Material and Methods

2.1. Experiments

Achenes of *A. montana* and *C. dissectum* were collected from a natural population in Dutch nature reserves (*A. montana*: Schoapedobbe, 52°57′ N, 6°15′ E; *C. dissectum*: 52°21′ N, 7°04′ E). Achenes were stored under dry and dark conditions at room temperature until the start of the experiment. Achenes were germinated in petri-dishes, on filter paper wetted with demineralised water at room temperature.

Because of the very low growth rate of *Calluna vulgaris*, shoot cuttings were used in stead of seedlings. These were collected in August 1993 from a natural heathland population (Schoapedobbe, 52°57′ N, 6°15′ E) and grown on nutrient solution (without Al; see below) for 63 days in order to root. The rooted cuttings of *C. vulgaris* (shoot length approximately 6 cm; root length approximately 2 cm) were transferred to opaque containers (2 l), as were the seedlings of *A. montana* and *C. dissectum* (root length approximately 2 cm). The nutrient solution of each container was continuously refreshed, using 10 l medium per week. Aerobic conditions were

Table I

Aluminium and calcium concentrations in the nutrient solutions (in μmol l^{-1}). Aluminium was added as $AlCl_3$, calcium as $CaCl_2 \cdot 2H_2O$. In addition, NaCl was added in order to correct for ionic strength

Medium	Al	Ca	NaCl
A	0	100	1500
B	50	100	600
C	100	100	300
D	200	100	150
E	500	100	0
F	100	1000	0
G	500	5000	0

maintained by a continuous flow of air through the containers. Plants were grown in a climate chamber at a day/night (14/10 h) temperature of 28/16 °C, a light intensity of approximately 100 μE $m^{-2}s^{-1}$ and with a relative humidity of 50–65%. For all species, three replicates per treatment were included, except for the 50/100 Al/Ca-treatment for *A. montana*, where n = 6. This is due to the fact that the experiment with *A. montana* was performed in two groups, in both of which the 50/100 Al/Ca treatment was included. No significant differences between the 50/100 Al/Ca treatments of both groups were found in either parameter that has been tested.

Seven Al and Ca treatments were supplied (Table I) with Al varying from 0 to 500 μmol l^{-1} and Ca from 100 to 5000 μmol l^{-1}. Treatments with low calcium concentrations were corrected for ionic strength and chloride concentration by the addition of NaCl (Table I). Other nutrients were added in the following concentrations: 100 μM KNO_3, 100 μM $MgCl_2 \cdot 6H_2O$, 100 μM $Na_2HPO_4 \cdot 2H_2O$, 100 μM KH_2PO_4, 70 μM Fe-EDTA, 0.7 μM $ZnSO_4 \cdot 7H_2O$, 0.8 μM $MnCl_2 \cdot 4H_2O$, 0.2 μM $CuSO_4$, 0.008 μM $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$, 0.8 μM H_3BO_3 and 0.3 μM thiamin hydrochloride. In experiments with *C. vulgaris*, 100 μM $(NH_4)_2SO_4$ was added in addition, because of the preference of *C. vulgaris* for NH_4 as a N source (Houdijk and Roelofs, 1993). For compensation of sulphate, only 450 μM Na_2SO_4 was added to the nutrient solutions in the *Calluna*-experiments, whereas the nutrient solutions in the experiments with *A. montana* and *C. dissectum* contained 500 μM Na_2SO_4. The media were adjusted twice a week at pH = 4.00 by HCl, in order to remain Al^{3+} in the ionic state. Never was any precipitate found in the storage or growth containers. In the plant containers, pH was allowed to fluctuate as result of the treatment; however, in the aluminium-containing treatments, pH generally remained below 4.20. In the treatments were no Al was added, pH increased to a mean value of 4.32.

The following numbers of plants were grown per container: *A. montana*: 9; *C. dissectum*: 6; *C. vulgaris*: 5. *C. dissectum* and *A. montana* were harvested after respectively 28 and 63 days, when competition for light became obvious. Because of its low growth rate, *C. vulgaris* plants were harvested after 95 days. At harvest, shoots and roots were separated and the dry weight of the shoots and roots was measured after drying at 70 °C for 24 h. The shoots were pooled per container for nutrient analyses as were roots, whenever enough plant material was available. Both were ground with liquid N_2 and dried again (70 °C, 24 h). The plant material was digested in 5 ml concentrated H_2SO_4 and 2 ml 30% H_2O_2 (Van Dijk and Roelofs, 1988). The concentrations of Al, Ca, Mg and phosphorus (P) were determined using an ICP (type IL Plasma 200). N contents were measured colometrically with a continuous flow autoanalyser (Technicon AAII system). Due to equipment failure, we were not able to analyse all *A. montana* plants for N.

2.2. Statistical analysis

Data were statistically analysed using a GLM procedure after testing for normality; multiple comparisons among pairs of means were made using the Tukey's studentized range test. Plant dry weight was log transformed before testing, in order to fit a normal distribution. All statistical analyses were performed using SAS 6.0.

3. Results

3.1. Shoot and root biomass

The dry weight of shoot and roots of *A. montana* decreased gradually with increasing Al concentration and constant Ca concentration (100 μmol l^{-1}) in the nutrient solutions (Figure 1). The shoot dry weights were significantly lower in the 200 and 500 μmol Al l^{-1} treatments, whereas root biomass was only significantly lower at 500 μmol Al l^{-1}, compared with the control treatment (without Al). The shoot and root biomass of *C. dissectum* increased after the addition of 50 μmol Al l^{-1} in the nutrient solution, compared with the control treatment. At higher Al concentrations (with 100 μmol Ca l^{-1}), the shoot and root biomass decreased, however, considerably. Compared with the 50 μmol l^{-1} Al treatment, the root dry weights were significantly lower when 200 μmol l^{-1} Al or more was added to the nutrient solution. The shoot dry weight of this species decreased only significantly in the 500 μmol Al l^{-1} treatment.

The negative effects of Al on the dry weights of *A. montana* and *C. dissectum* were, although not significantly, diminished when Ca concentrations in the solutions were raised to 1000 or 5000 μmol l^{-1}, compared with the treatment with the same Al concentration but low Ca concentration.

Plant growth of the *C. vulgaris* cuttings occurred during the experimental period: in all treatments new branches and leaves were formed. The dry weights of

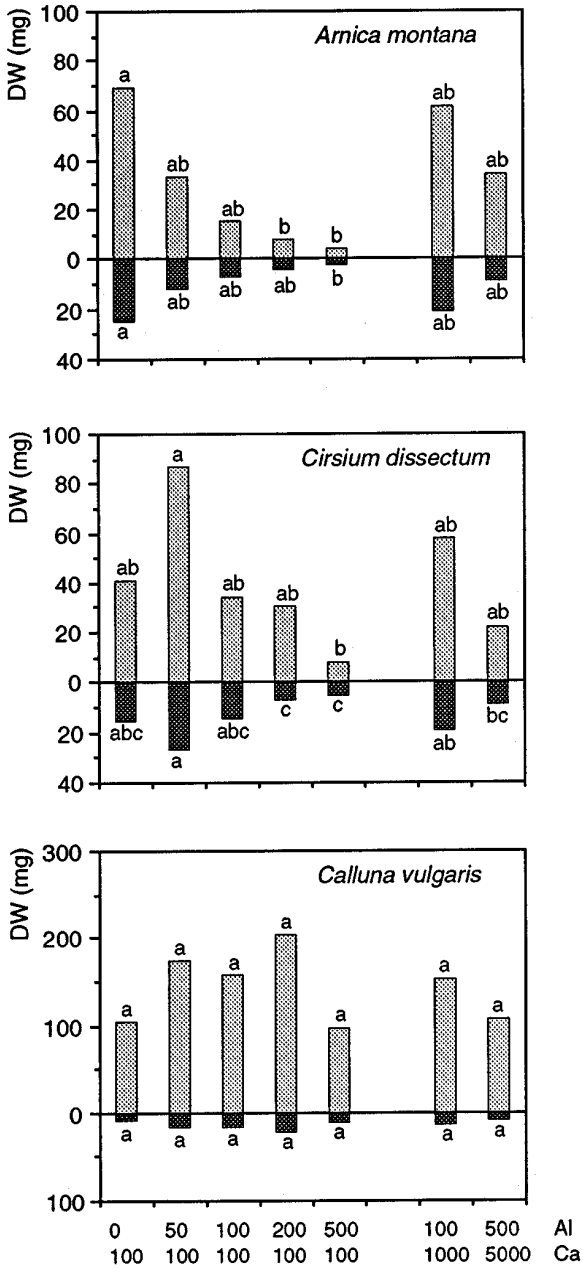

Figure 1. Mean root (dark) and shoot (light) dry weight of *A. montana, C. dissectum* and *C. vulgaris* treated with different concentrations of Al (0, 50, 100, 200 or 500 μmol l^{-1}) and Ca (100, 1000 or 5000 μmol l^{-1}). Significant differences within species are indicated by different letters ($p<0.05$; N = 3). Significant differences in total plant dry weight follow differences in shoot dry weight for *A. montana* and *C. vulgaris*; for *C. dissectum* total dry weight was higher of plants grown on 50 μmol l^{-1} Al than dry weight of plants grown on 200 or 500 μmol l^{-1}, regardless of Ca concentration.

the shoots and roots of *C. vulgaris* were, however, not affected by the different aluminium or calcium treatments (Figure 1).

The habit of *A. montana* and *C. dissectum* was also affected by increased Al concentrations; the leaves became yellow and the root development stunted. These symptoms of reduced vitality were observed in *A. montana* in solutions with 50 μmol Al l^{-1} or more, and in *C. dissectum* in solutions with 100 μmol Al l^{-1} or more. Plants of both species which were grown on a nutrient solution with 100 μmol Al l^{-1} and 1000 μmol Ca l^{-1}, did not show the symptoms of reduced vitality; when 500 μmol Al and 5000 μmol Ca l^{-1} was applied, plants were again less vital. The just-described symptoms of reduced vitality were not observed in the plants of *C. vulgaris*, although the root system of this species was best developed in nutrient solutions with 100 or 200 μmol Al l^{-1} or more, and low Ca concentrations.

3.2. Nutrient concentrations in the shoots and roots

The nutrient concentrations in the roots of the three investigated heathland species were hardly influenced by the Al treatments, but differences in the nutrient concentrations of the shoots were observed (Table II). In all three species Al accumulated in the shoots when the Al concentrations in the nutrient solution increased. This increase was largest in *A. montana*-shoots, folowed by *C. dissectum* and *C. vulgaris* respectively. Shoot Al concentrations of *A. montana* and *C. vulgaris* were not reduced by addition of 1000 or 5000 μmol Ca l^{-1} to the nutrient solution. Addition of 5000 μmol Ca l^{-1} seemed to reduce the Al concentrations in the shoot material of *C. dissectum*, although the reduction was not significant. All three species showed higher Ca concentrations in the shoots when the plants were grown on nutrient solutions with high Ca concentrations, but no effects of increased Al supply on shoot Ca concentrations were observed. Mg concentrations in the shoot material of *C. dissectum* were, not significantly, reduced in the 500 μmol Al L^{-1} treatment. In the 100:1000 and 500:5000 Al:Ca treatments of *C. dissectum*, the Mg contents in the shoots were lower than in treatments with similar Al concentrations and 100 μmol Ca l^{-1}. Mg concentrations in the shoots of *A. montana* and *C. vulgaris* were not affected by the different treatments (Table II).

P concentrations of the roots of the three investigated species have not been influenced by any of the treatments. The P concentrations in the shoots of *C. vulgaris* were neither affected by the Al or Ca addition. The P concentrations in the shoots of *A. montana*, which were grown at 500 μmol Al l^{-1}, decreased significantly compared with the control treatment and almost independent of the applied Ca concentrations. In *C. dissectum* shoots P concentrations were, however, significantly higher in the 200 μmol Al l^{-1} treatment, compared with plants which had been supplied with 50 or 500 μmol l^{-1} Al. No effects of Al treatments on N concentrations in shoots or roots of the three investigated species were found. The Ca addition of 500 μmol or 5000 μmol l^{-1} significantly decreased the N

Table II

Mean nutrient concentration in leaf and root of *A. montana*, *C. dissectum* and *C. vulgaris* (in μmol g^{-1}). Significant differences between treatments are indicated by different letters ($p<0.05$)

	Al = 0 Ca = 100		Al = 50 Ca = 100		Al = 100 Ca = 100		Al = 200 Ca = 100		Al = 500 Ca = 100		Al = 100 Ca = 1000		Al = 500 Ca = 5000	
A. montana, shoot														
Al	3.7	a	56	ab	96	ab	148	ab	234	b	75	ab	207	ab
Ca	125	a	109	a	84	a	72	a	83	a	463	b	775	c
Mg	121	a	66	a	96	a	83	a	75	a	74	a	204	a
P	621	ac	665	a	672	a	493	ab	231	b	462	ab	291	bc
N	*		1786	a	*		*		*		1759	a	1231	b
n	3		6		3		3		3		3		2	
C. dissectum, shoot														
Al	<0.2	a	<0.2	a	24	ac	181	b	112	bcd	25	ad	23	ad
Ca	239	a	227	a	237	a	295	a	123	a	661	b	970	b
Mg	212	ab	203	ab	204	ab	290	b	88	ac	80	ac	17	c
P	178	ab	154	a	206	ab	379	b	136	a	195	ab	70	a
N	937	a	711	a	1409	a	736	a	442	a	589	a	223	a
n	2		3		2		3		3		3		3	
C. vulgaris, shoot														
Al	6	a	26	ab	28	ab	43	ab	84	b	24	ab	46	ab
Ca	70	ab	67	a	84	ab	63	a	63	a	243	ab	293	b
Mg	55	a	67	a	79	a	70	a	62	a	67	a	48	a
P	99	a	142	a	137	a	128	a	117	a	115	a	109	a
N	973	a	1149	a	1234	a	1272	a	1216	a	1122	a	1391	a
n	3		3		2		3		3		3		2	
A. montana, root														
Al	90	a	218	a	239	a	224	a	273	a	319	a	223	a
Ca	343	a	94	a	66	a	111	a	147	a	108	a	21	a
Mg	124	a	214	a	77	a	99	a	162	a	318	a	214	a
P	709	a	924	a	758	a	778	a	945	a	636	a	218	a
N	*		1532	a	*		*		*		1429	ab	806	b
n	3		6		3		3		3		3		1	
C. dissectum, root														
Al	<0.2	a	60	a	163	a	189	a	144	a	121	a	81	a
Ca	65	a	104	a	32	a	23	a	36	a	58	a	58	a
Mg	31	a	47	a	33	a	24	a	11	a	34	a	0	a
P	165	a	268	a	499	a	472	a	182	a	452	a	187	a
N	493	a	610	a	536	a	339	a	55	a	475	a	105	a
n	2		1		2		3		3		3		3	

(table continues on next page)

Table II
Continued.

	Al = 0 Ca = 100		Al = 50 Ca = 100		Al = 100 Ca = 100		Al = 200 Ca = 100		Al = 500 Ca = 100		Al = 100 Ca = 1000		Al = 500 Ca = 5000	
C. vulgaris, root														
Al	15	a	319	ab	263	ab	256	ab	412	b	272	ab	157	ab
Ca	11	a	11	a	40	a	21	a	41	a	28	a	20	a
Mg	60	a	24	a	72	a	52	a	63	a	73	a	34	a
P	189	a	308	a	374	a	406	a	521	a	438	a	225	a
N	1965	a	1106	a	1752	a	1759	a	2396	a	1748	a	1129	a
n	2		2		2		3		3		2		1	

n = Number of replicates, * = Not determined.

concentrations in the leaves of *A. montana* (Table II), but due to equipment failure we were unable to determine N concentrations of the shoots in all treatments.

4. Discussion

In many studies the toxicity of Al for plant species has been investigated on water culture. In order to relate the results to the field situation, it is essential that the nutrient solutions which are used resemble the soil solution as best as possible (Andersson and Brunet 1993; Sverdrup and Warfvinge, 1993; Falkengren-Grerup, 1994). In heathland ecosystems, nutrient concentrations of the soil are very low. The nutrient concentrations that we have used in this experiment are in good agreement with field measurements, except for P and K (data not shown). These were somewhat higher in the nutrient solution than in the field (Table II, Matzner and Ulrich, 1980; Hayati and Proctor, 1990; Houdijk *et al*., 1993; De Graaf *et al*., 1994).

The growth of *A. montana* and *C. dissectum* was negatively affected by Al concentrations of 100 μmol $l^{-1}$and more, whereas growth of the dwarf-shrub *C. vulgaris* was not affected at all. Symptoms of reduced vitality, e.g. stunted root growth and changes in chemical plant composition, have also been observed with increasing Al concentrations for *A. montana* and *C. dissectum.* In *A. montana*, the most Al-sensitive species, root development was already influenced at 50 μmol Al l^{-1}. Stimulation of plant growth by low Al concentrations, as in *C. dissectum* in this experiment, has been observed for more species (Foy, 1978). Hackett (1965) showed that growth of *Deschampsia flexuosa*, a characteristic grass species of acidic habitats, is also stimulated by low Al concentrations.

Our results concerning the effects of Al on *A. montana* do not agree with those found by Pegtel (1987) and Kroeze *et al*. (1989). They concluded that the growth of *A. montana* on water culture was not influenced by Al, not even at Al concentrations of almost 3000 μmol l^{-1}. However, already at intermediate Al concentrations Pegtel

(1987) observed reduced root elongation, a reduction in fine-branching of the roots, yellowish-green leaves and the development of necrotic spots on the leaves. This indicates that plants are affected by the treatment; particularly the mentioned root morphology is characteristic of Al toxicity (Foy *et al*., 1978). The difference in the sensitiveness of *A. montana* to Al is most likely caused by the very high nutrient concentrations (especially N: 4000 μmol l^{-1} and K: 2330 μmol l^{-1}) in the media used by Pegtel (1987) and Kroeze *et al*. (1989) and the lower, more realistic concentrations used in this experiment (N: 100 μmol l^{-1}, K: 600 μmol l^{-1}). The high nutrient concentrations in solutions might enable sufficient nutrient uptake by plants, even when root vitality and nutrient uptake capacity are reduced by Al (Foy *et al*., 1978).

Chemical composition of plants differs between roots and shoots and between species and can be influenced by environmental stresses. A commonly observed phenomenon of high Al concentrations in soil or nutrient solutions is the accumulation of Al in the plant (Foy *et al*., 1978). In this study, Al concentrations in all three heathland species clearly increased with increasing Al concentrations in the nutrient solution (Table II). This increase in Al concentrations in the shoots correlated with the decrease in plant biomass of *A. montana* and partly with the decrease in biomass of *C. dissectum*. Growth was not reduced in *C. vulgaris*. This species thus seems to resist high concentrations of Al in the shoot, whereas the other investigated species are affected by these Al concentrations. High Al concentrations in nutrient solutions are known to influence the uptake of minerals; particularly the uptake of the divalent cations Ca and Mg is often disturbed by Al (Foy *et al*., 1978, for a recent review see Delhaize and Ryan, 1995). However, none of the three heathland species showed significant decreases in Ca concentrations in roots or shoots, while the Mg concentration was only decreased in the highest Al treatment in the shoots of *C. dissectum* (Table II). This strongly suggests that the detrimental effects of Al in this study are not primarily caused by reduced cation uptake.

N and P are the main growth limiting factors in nutrient-poor habitats. Al significantly reduced plant P concentrations in the two species sensitive to Al (Table II). P deficiencies sometimes appear as a result of Al toxicity (Foy, 1978). It is, however, unlikely that the observed effects of Al on plant growth in this experiment are caused by P deficiency, because even in the highest Al treatment P concentrations in the plant are considerably higher than those of natural populations (Hayati and Proctor, 1990; Pegtel, 1994).

Negative effects of Al on growth and plant vitality were partly ameliorated in *A. montana* and, to a lesser degree, *C. dissectum* by high Ca concentrations. The beneficial effects of Ca on Al toxicity in plants have been recognized for a long time, although the mechanism by which Ca reduces Al toxicity is not yet fully understood (Rengel, 1992; Kinraide *et al*., 1994; Ryan *et al*., 1994). Recent research by Ryan *et al*. (1994) shows that Ca primarily reduces the negative effects of Al on root elongation, not on Ca uptake. Despite this, the Ca concentrations in the

above-ground parts of *C. dissectum* and *A. montana* are significantly raised by the addition of 1000 or 5000 μmol Ca L^{-1} to the nutrient solution in this experiment. A correlation between Ca in the soil solution and plant uptake was also found in the field for *C. dissectum* by Hayati and Proctor (1990). This increase in Ca concentrations in *A. montana* and *C. dissectum* correlated partly with the increase in biomass production and improved vitality of the plants. Still, the detrimental effects of Al cannot be fully reversed by high Ca concentrations (Figure 1), indicating that high concentrations of Al are toxic themselves to these two species.

Another cause for the reduced growth of *C. dissectum* on 5000 μmol Ca l^{-1} and 500 μmol Al l^{-1} might be this very high Ca concentrations in the nutrient solution, which reduce Mg concentrations in the shoots. Schimansky (1991) reported a similar negative effect of high Ca concentrations in the nutrient solutions, which added to the effects of Al toxicity.

4.1. Ecological implications

Plants in acidic habitats have to deal with extreme soil properties: high hydrogen and aluminium concentrations, low calcium concentrations, relatively high manganese and ferrous concentrations and high ammonium to nitrate ratios (Runge and Rode, 1991). The results of this experiment reveal the sensitivity of *A. montana* and *C. dissectum* to Al concentrations >100 μmol l^{-1}. This could be one of the major causes for the recent decline of these species. The observed sensitivity is in good agreement with the results of pot experiments of Heijne (1995) and with those of a field survey by Fennema (1992) on *A. montana*. The latter showed that sites from which *A. montana* had recently became extinct, had higher exchangeable Al concentrations than sites where the species was still present. Since all the tested plants developed well in our experiments at pH = 4.0, when they were grown on nutrient solutions containing 50 μmol l^{-1} Al or less, we assume that toxicity of hydrogen ions is not important for *A. montana, C. dissectum* or *C. vulgaris*.

Our results indicate furthermore that low Ca concentrations in soil might be a problem for *A. montana* and *C. dissectum*. Both species have distinctly higher Ca concentrations in the shoot than *C. vulgaris* (Table 1, Hayati and Proctor, 1990; Pegtel, 1994). Again, these findings confirm the limited adaptation of *A. montana* and *C. dissectum* to acidifying conditions, where *C. vulgaris* is more tolerant to the acidic conditions.

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References

Aerts, R.: 1993, in R. Aerts and G. W. Heil (eds.) *Heathlands: Patterns and Processes in a Changing Environment*, Dordrecht, Kluwer Academic Publishers.

Aerts, R. and Berendse, F.: 1988, *Vegetatio* **76**, 63.

Andersson, M. E. and Brunet, J.: 1993, *Plant Soil* **153**, 243.

Bobbink, R., Boxman, D., Fremstad, E., Heil, G., Houdijk, A. and Roelofs, J.: 1992, *Critical Loads for Nitrogen Eutrophication of Terrestrial and Wetland Ecosystems Based Upon Changes in Vegetation and Fauna*. Nordic Council of Ministers, Copenhagen, Miljörapport, 41, 111–159.

Boxman, A. W., Krabbendam, H., Bellemakers, M. J. S. and Roelofs, J. G. M.: 1991, *Environ. Pollut*. **73**, 119.

De Graaf, M. C. C., Verbeek, P. J. M., Cals, M. J. R. and Roelofs, J. G. M.: 1994, *Effectgerichte maatregelen tegen verzuring en eutrofiëring van matig mineraalrijke heide en schraallanden*. University of Nijmegen, The Netherlands.

Delhaize, E. and Ryan, P. R.: 1995, *Plant Physiol*. **107**, 315.

Dueck, T. A. and Elderson, J.: 1992, *New Phytol*. **122**, 507.

Falkengren-Grerup, U.: 1994, *J. Appl. Ecol*. **31**, 182.

Fennema, F.: 1992, *Water, Air, and Soil Pollut*. **62**, 325.

Foy, C. D., Chaney, R. L. and White, M. C.: 1978, *Annu. Rev. Plant Physio*. **29**, 511.

Hackett, C.: 1965, *J. Ecol*. **35**, 299.

Hayati, A. A. and Proctor, M. C. F.: 1990, *J. Ecol*. **78**, 134.

Heil, G. W. and Diemont, W. H.: 1983, *Vegetatio* **53**, 113.

Heijne, B., Van Dam, D., Heil, G. W. and Bobbink, R.: 1995, in *Effects of Acid Rain on Vesiculair-Arbuscular Mycorrhiza of Herbaceous Plants in Dry Heathland*, PhD-Thesis, University of Utrecht, The Netherlands.

Houdijk, A. L. M. F. and Roelofs, J. G. M.: 1993, in *Atmospheric Ammonium Deposition and the Nutritional Balance of Terrestrial Ecosystems*, PhD-Thesis, University of Nijmegen, The Netherlands.

Houdijk, A. L. F. M., Verbeek, P. J. M., Van Dijk, H. F. G. and Roelofs, J. G. M.: 1993, *Plant Soil* **148**, 137.

Kinraide, T. B., Ryan, P. R. and Kochian, L. V.: 1994, *Planta* **192**, 104.

Korcak, R. F.: 1990, in M. L. van Beusichem (ed.), *Plant Nutrition – Physiology and Applications*, Dordrecht, Kluwer Academic Publishers.

Kroeze, C., Pegtel, D. M. and Blom, C. J. C.: 1989, *Acta Bot. Neerl*. **38**, 165.

Matzner, E.: 1980, *Untersuchungen zum Elementhaushalt eines Heide-Ökosystems (Calluna vulgaris) in Nordwestdeutschland*, Thesis, University of Göttingen, Germany.

Matzner, E. and Ulrich, B.: 1980, *Z. Pflanzenernäerh. Bodenkd*. **143**, 666.

Pegtel, D. M.: 1987, *Plant Soil* **102**, 85.

Pegtel, D. M.: 1994, *Vegetatio* **114**, 109.

Rengel, Z.: 1992, *New Phytol*. **121**, 499.

Roelofs, J. G. M.: 1986, *Experientia* **42**, 372.

Runge, M. and Rode, M. W.: 1991, in B. Ulrich and M. E. Sumner (eds.), *Soil acidity*, Berlin, Springer Verlag.

Ryan, P. R., Kinraide, T. B. and Kochian, L. V.: 1994, *Planta* **192**, 98.

Schimansky, C.: 1991, *Z. Pflanzenernäerh. Bodenkd*. **154**, 195.

Sverdrup, H. and Warfvinge, P.: 1993, *The Effect of Soil Acidification on the Growth of Trees, Grass and Herbs as Expressed by the (Ca+Mg+K)/Al Ratio*, Reports in ecology and environmental engineering, Lund.

Ulrich, B.: 1983, in Ulrich, B. and Pankrath, J. (eds.) *Effects of Accumulation of Air Pollutants in Forest Ecosystems*, Reidel Publ. Comp., Dordrecht, The Netherlands.

Van Dam, D., Van Dobben, H. F., Ter Braak, C. F. J. and De Wit, T.: 1986, *Vegetatio* **65**, 47.

Van Dijk, H. F. G. and Roelofs, J. G. M.: 1988, *Physiol. Plant*. **73**, 494.